

totally differs in habit and form. The opacity of the cell prevented me from discerning whether it has a gizzard.

EXPLANATION OF PLATES III. AND IV.

PLATE III.

- Fig. 1. *Halacarus rhodostigma*, magnified, ventral surface.
 — 2. *Ibid.* dorsal surface of trunk.
 — 3. *Ibid.* rostrum and palpi.
 — 4. *Ibid.* punctures of surface.
 — 5. *Ibid.* unguis of foot.
 — 6. *H. ctenopus*, magnified, dorsal surface.
 — 7. *Ibid.* ventral surface.
 — 8. *Ibid.* rostrum and palpi.
 — 9. *Ibid.* right palpus.
 — 10. *Ibid.* one unguis of a foot.
 — 11. *Cyamus Thompsoni*, magnified, ventral surface.
 — 12. *Phoxichilidium olivaceum*, nat. size.
 — 13. *Ibid.* fore-parts magnified.

PLATE IV.

- Fig. 14. *Syllis longiseta*, in its tube, nat. size.
 — 15. *Ibid.* magnified.
 — 16. *Ibid.* head, somewhat laterally.
 — 17. *Ibid.* a right foot seen from behind.
 — 18, 19. *Ibid.* setæ of the upper pencil.
 — 20. *Ibid.* a middle segment, from above.
 — 21. *Ibid.* the same, from below.
 — 22. *Othonia Fabricii*, magnified.
 — 23. *O. Bairdii*, magnified.
 — 24. *Ibid.* a pencil of setæ, more enlarged.
 — 25. *O. Johnstoni*, nat. size.
 — 26. *Ibid.* magnified (middle segments omitted).
 — 27. *Ibid.* bristles of two forms.
 — 28. *Ibid.* a portion from a stem of the gills, with two pinnae.
 — 29. *Nolella stipata*, magnified.

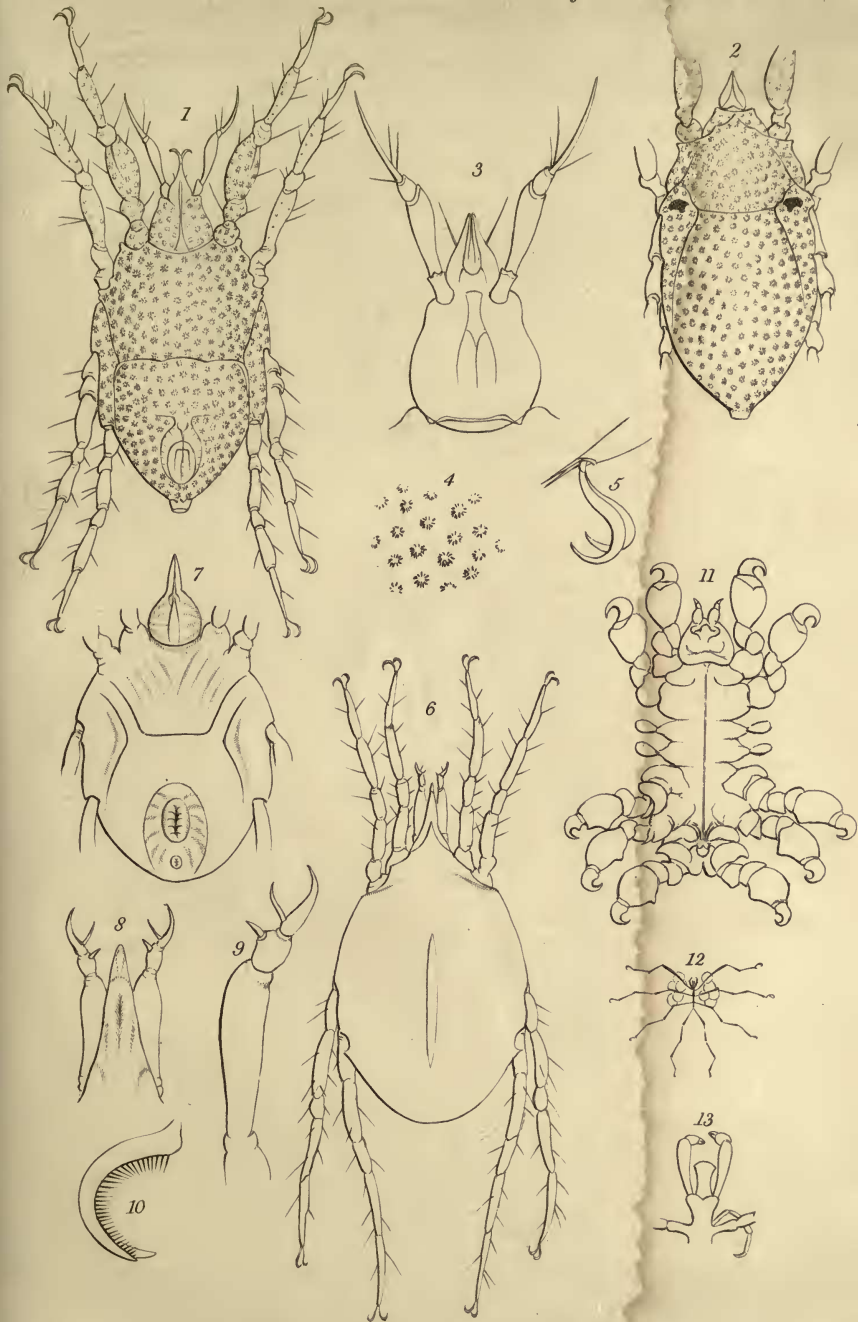
IV.—On the Homologies of the Carapace and on the Structure and Function of the Antennæ in Crustacea. By C. SPENCE BATE, F.L.S. &c.*

[With two Plates.]

IN the class Crustacea the most anterior articulation is that which supports the eyes. This is shown most conspicuously in the genus *Squilla*, in which animal it is united by a free joint with the next succeeding; but if this lucid example were wanting, the relative position of the ophthalmic ring in advance of any of the rest is clearly manifest in the larva and pupa stages of the Decapoda.

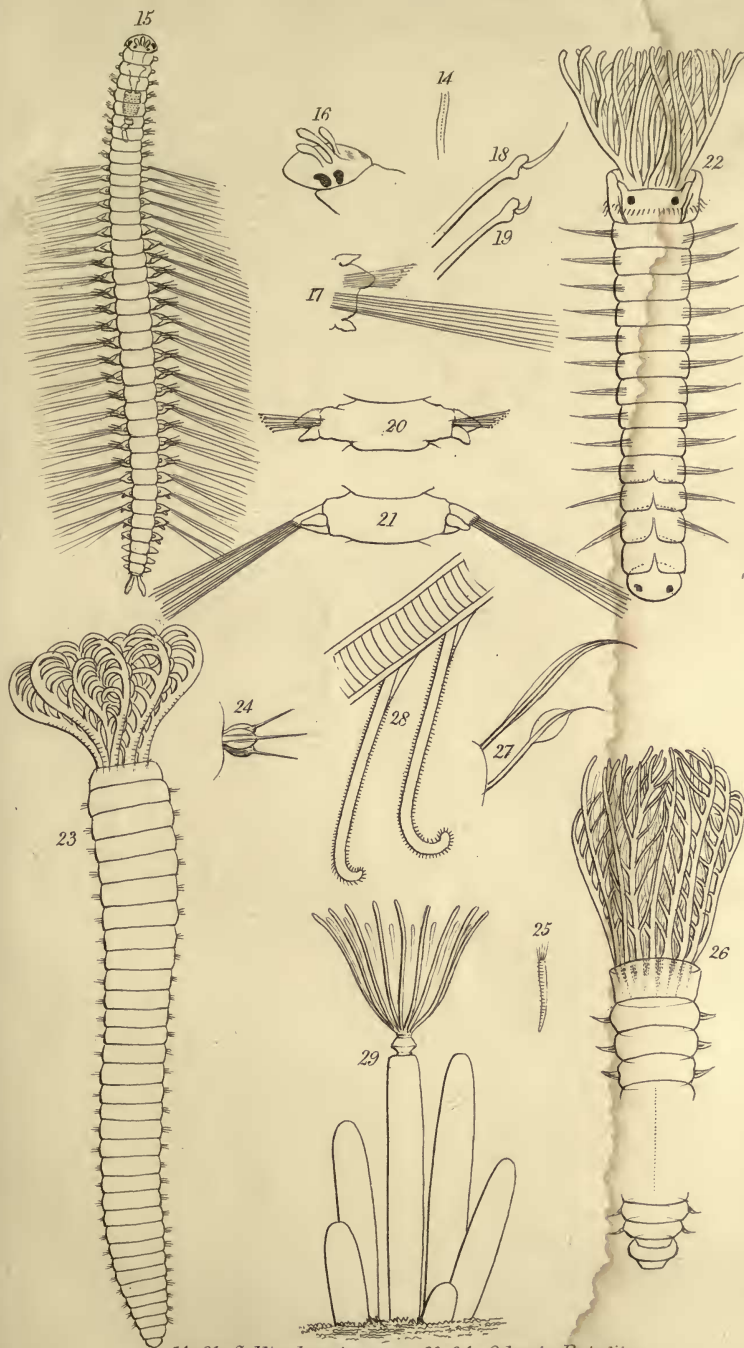
Dissection moreover leads to the same conclusion. Upon

* Communicated by the author, having been read at the Linnaean Society, April 17, 1855.



1-5. *Halacarus rhodostigma*. 11. *Cyamus Thompsoni*
 6-10. *Halacarus ctenopus*. 12. 13. *Phoxichilidium olivaceum*.





14-21. *Syllis longiseta*. 23. 24. *Othonia Bairdii*.
 22. *Othonia Fabricii*. 25-28. *O. Johnstoni*.

29. *Nolella stipata*.



laying bare the cephalic ganglion, we find that the two anterior branches of nerves pass to the eyes, the central being the *motor oculi*, the outer the *ophthalmic*, and lead direct to the organs of vision.

In all the higher tribes, except the aberrant family of *Diastylidæ* (Say) (*Cuma* of M. Milne-Edwards), the eyes are borne on moveable pedicles. In the *Brachyura* the ring which bears these pedicles is free, but unlike *Squilla*, instead of being seen distinctly in advance of the animal, it is enclosed within and covered by the anterior portion of the carapace; I say that it is *covered* by, and not absorbed into, the structure of the integument which forms the anterior portion of the external skeleton of these animals.

If we throw off the carapace we shall find that the calcareous representation (Pl. I. fig. 1 *a*) of the ophthalmic ring occupies a position between and connecting the two eyes, lodged in a fossa (Pl. I. fig. 2 *w*) formed by the interspace between the dorsal and ventral arches of the second ring, the superior antennal, which arches approximate in the *Brachyura* so closely, that, as in the genus *Cancer*, they meet in front of and enclose the ophthalmic ring, leaving the point of union visible only by a distinct suture (Pl. I. fig. 3 *a*). Thus the ophthalmic ring is covered by and not fused with the rest of the testaceous skeleton;—it therefore takes no part in the development of the carapace of the Decapod Crustacea.

The superior antennæ succeed the eyes, and with the exception of the genus *Squilla*, the ring which supports them is always fused with the succeeding, the inferior antennal. These two form a closely associated part in the anterior structure of the animal, and together build up the whole of that portion of the carapace which is in advance of the cervical suture, and which, I think, I shall be able to show, forms almost the whole of the carapace in the *Brachyura*,—half of the same in *Macroura*,—and that it lessens in importance as the animal descends in the scale of nervous centralization.

If we turn our attention to the lower forms, we find that in the *Cuma* and other allied genera of the *Diastylidæ*, the eye (for the two coalesce so as to form but one) is developed nearly in the centre of the carapace; but this appearance is only the result of the great development of the lateral angles of the carapace, which meet in front and form what appears like a rostrum; they never unite, but are distinctly separated through the centre of the so-called rostrum, as well as on either side of that portion which supports the antennal rings, which occupies a small island as it were in the centre of the carapace (Pl. I. figs. 4, 5 & 6).

The fact which dissection has enabled us distinctly to make

out, that the small central patch bears the two antennæ, that the external angles of the carapace which pass in front and surround it posteriorly, carry the mandibles, demonstrates the relation of one portion of the carapace to the other, and that the line of separation round the antennal centre homologizes with the cervical suture of the *Macroura*.

The constant position of this suture in all Crustacea when present is the same, and forms a line of demarcation between the third and the fourth rings, and therefore visible in its position external to the inferior antennæ; and M. Milne-Edwards is most assuredly wrong when he attributes the depressions on the carapace, which terminate in the central notch of the orbits of the *Brachyura*, to be the representatives of the cervical suture of the *Macroura*.

If we wish to judge of its position in the *Brachyura*, it is but just that we should make a careful investigation of the structure of the animal in its immature condition. In the so-called pupa stage of the Crab, we find that the inferior antennæ are attached to the extreme horns of the carapace (Pl. I. fig. 7), but these horns are folded beneath the animal; it is this reflexion which afterwards forms the orbit in which the eye is lodged.

The position of the antenna, anchylosed as it is with the dermal skeleton in all the *Brachyura*, still holds the same, therefore by inversion the cervical suture must be inferiorly inside, but still within the limits of the carapace; such a suture is plainly demonstrable in most of the *Brachyura* (Pl. I. fig. 10, and Pl. II. fig. 1), and separates the inferior antennal (*a*) from the mandibular ring (*b*); it extends posteriorly to the extreme limits of the carapace, forming as it were two side pieces, the epimerals of M. Milne-Edwards: this line unquestionably homologizes with the cervical suture of the *Macroura*.

If we turn our attention to the development of the nervous system in these various animals, we shall find that centralization decreases in an inverse ratio with the development of that portion of the carapace which is posterior to the cervical suture, and *vice versâ*, that centralization is most perfect when that portion of the carapace which is anterior to the cervical suture is largest.

In the *Brachyura* the nervous ganglia are in the highest degree consolidated, and in the Spider Crabs the most perfect centralization exists; there we shall find that the cervical suture, the line of union between the inferior antennal and mandibular rings, is so lateral, that the two side pieces of the incomplete mandibular ring are reduced to much less importance than is to be found in any other tribe of the whole class. In the genus *Cancer*, &c. the line of union remains but partially anchylosed, and splits when the animal throws off its exuvizæ.

In the *Galatheadæ*, the development of the mandibular ring shows a closer approximation to the *Brachyura* than to the *Macroura*, in which latter the two antennal rings occupy but one-half of the whole carapace, the mandibular ring furnishing the remainder; whereas the *Paguridæ* assimilate closer in the development of the same portion to the *Macroura*,—a circumstance in its position among Crustacea corroborated by the fact, that previous to their taking possession of the shell of the mollusca, they exhibit all the characteristics of a perfect *Macroura*. Here, when the nervous centre commences its first tendency to separate into numerous distinct but less important ganglia, we find those rings which carry distinct organs of sense, and furnished by nervous filaments from the cephalic ganglion, decrease in a relative proportion to the rest of the animal: this, which we see very apparent in the *Macroura*, is carried to the greatest extent in the *Diastylidæ*, where the carapace is constructed almost wholly of the mandibular ring, having but a small area in the centre which bears the antennæ. And more, the carapace extends posteriorly so as to envelope only the Gnathopods; the rest of the thorax being complete in the development of each separate ring.

Lower in the scale we find that the whole thorax, including the Gnathopods, is perfect in its distinction from the cephalic ring, which latter is so reduced in importance as to differ little in appearance from that of a single ring; whereas consolidation still remains, and embraces within the compass of this one ring the whole of the seven anterior.

But we have seen in the descending scale of nervous force the rings which carry the organs of consciousness degenerate in importance, and yield to a corresponding development of the mandibular ring; this law appears still to be in force in the Amphipoda, the lowest type of the *Macroura* form, in which I am inclined to believe that the mandibular ring represents the whole of the upper portion of the cephalic articulation; the anterior three being so diminished in importance, that they are to be found only in the perpendicular anterior wall of the head*, or perhaps represented by their appendages only.

Since the present paper was communicated to the Linnæan Society, the author has had the opportunity, through the kindness of Mr. J. Lubbock, of perusing Dana's great work on Crustacea, and it is but just he should state, that the conclusions, which careful and long-continued observation of the homologies

* An example of which may be seen in the manner in which the two first joints of the external antennæ are absorbed in the frontal aspect of *Talitra*; a circumstance overlooked by naturalists, who have invariably described this genus as having but three instead of the constant five articulations to the peduncle of the inferior antennæ.

of the carapace of Crustacea had induced him to arrive at, are in some of the most important points anticipated in the work of the United States' Exploring Expedition.

But since they have been arrived at by independent research, the regret with which the author found his deductions forestalled, are to a considerable extent removed by the important testimony of so learned and correct a naturalist as Mr. Dana. The following two sentences are taken from the first volume of that author; the italics being in the original text:—

“We are therefore led to believe, *that the so-called epimerals, or ventral pieces of the carapax, are in fact the posterior extensions of the mandibular segment.*” (Page 27.)

Again—

“... Milne-Edwards thus makes the larger part of the carapax epimeral in character.

“Excepting that we consider what is here called epimeral, *the mandibular segment*, we agree with Edwards, for the most part, in the above-mentioned deduction; so that while the mandibular segment is confined to the ventral pieces of the Brachyural carapax, it constitutes its posterior half in *Macroura.*” (Page 32.)

The author also has had the opportunity at the British Museum of seeing the plates in Kroyer's great work on the Natural History of Scandinavia, where he finds the carapace of *Cuma Rathkii* (Kroyer) (the *Alauna rostrata* of Goodsir) is figured with the so-called rostrum separated from the antennal region, as drawn and described in this paper.

The Anterior or Internal Antennæ.

These organs are borne by the second ring, and supplied with nerves from the cephalic ganglion.

The anterior antenna is evidently of importance to the animal, and is always present in aquatic Crustacea: as a general law it consists of an articulated peduncle of three joints, which I believe I am correct in asserting, unlike those of the external antenna, are never anchylosed together or with the carapace, and a terminating filament, which is generally double, often treble, but I believe never single, above the Amphipoda. This appendage is various as well as unequal in length, and in every species that I have examined, whether in *Brachyura*, *Macroura*, Amphipod or Isopod, will invariably be found furnished, in addition to the small hairs common to other parts of the animal, with long, delicate, membranous cilia, in form varying in genera and species; they are always larger than the ordinary hairs, but much more delicate in structure. These vary in number and in thickness of clusters, but, as far as my experience goes, are invariably present on the upper antenna.

In the *Anomoura*, *Macroura*, and all below, the antenna gradually increases at the base. In the *Brachyura* this increase is immensely developed in the first or basal articulation. Examining this organ in the larva, I thought I observed what I took to be an otolithe*; this led my attention to the same in the adult *Brachyura*, and there I found, upon breaking open the basal articulation, what appeared to be an imperfect kind of cochlea. Afterwards, in company and with the assistance of my friend Mr. Howard Stewart, we were enabled to trace distinctly the nerve which supplied this antenna directly to the centre of the cochlea (for such I believe it is), as I feel convinced that the upper antennæ are auditory organs.

But since the general opinion up to the present time has been that they are olfactory and not auditory, and as the external antennæ are invariably considered as auditory and not olfactory, I shall withhold any further discussion until those organs have been described.

In the lower forms of *Podophthalmia*, as also in the Sessile-eyed Crustacea, the basal joint of the antenna is not enlarged, neither have I been enabled to find any structure answering to the internal cell; on the other hand, the whole organ increases in length, as if to gain by external surface what is lost by internal development.

Among the land Crustacea this antenna is obsolete, and in *Ligia* and other amphibious marine ones it is rudimentary.

The Inferior or External Antennæ.

These are borne upon the third ring, and are among the most constant organs present. One of these antennæ is formed of a peduncle consisting as a general law of five articulations and a filament, generally multiarticulate and very long; these are sometimes anchylosed together so as to be even as few as a single articulation.

The five joints of the peduncle are all distinct in the *Macroura*. In Amphipoda the first and second are closely associated, but

* In *Macroura*, Dr. Farre states that he found sand deposited in the base of the internal antenna, which he assumes to act the part of otolithes; this the author has failed to find, and, from the fact that the membrane over the orifice spoken of by Dr. Farre is imperforate, thinks it probable that the specimen examined by that observer must have been injured.

It may be, that in this communication sufficient justice is scarcely done to Dr. Farre's researches, since the short abstract published in the 'Annals' for 1843 has been the only means the author had at his disposal to become acquainted with them. But if, as he thinks, Dr. Farre's researches on the *Macroura* corroborate his on the *Brachyura*, then the evidence is strong against the generally received opinion of naturalists and physiologists, including among them Edwards and Siebold.

scarcely fused. In *Brachyura* the whole, more or less, certainly the four first, almost always coalesce, and are generally formed into a very compact mass, so that their position can only be indicated in *Sternorhynchus* by the presence of the olfactory operculum.

In the *Macroura* this operculum is absent, and an orifice protected by a thin membrane represents the position of the organ. In the Amphipoda the organ is developed in the form of a strong spine or tooth with an orifice at the extremity*. In the Isopoda I have not been able to decipher with confidence the organ of sense in the inferior antenna, but that it exists can scarcely be doubted, since the lower antenna, except in parasitic Crustacea, as the female of *Bopyrus* and *Iona*, is I believe never rudimentary.

The nerve which supplies this organ is a fifth pair or a branch of the fourth. In the *Brachyura*, in which our dissections have chiefly been made, the fourth pair of nerves extends beyond the inferior antenna, and then terminates in the muscles which raise and close the olfactory operculum.

This organ, which is described by M. Milne-Edwards as an organ of hearing, differs in its construction in the different families of Crustacea. In the *Brachyura* it is a small moveable appendage, situated at the point of articulation between the third and second joints; it is attached to a long calcareous lever-like tendon, at the extreme limit of which is attached a set of muscles by which it is opened and closed, to assist in which operation at the angle of the operculum most distant from the central line of the animal are fixed two small hinges. When the operculum is raised, the internal surface is found to be perforated by a small circular opening protected by a thin membrane.

Among the *Macroura* this orifice exists at the extremity of a small protuberance, and is not capable of being withdrawn into the cavity of the antenna, as in the *Brachyura*.

The next question which we have to consider is, to which sense either of these two sets of organs belongs;—whether the upper belongs to the auditory and the lower to the olfactory, as I shall endeavour to prove, or *vice versâ*, as maintained by Prof. Milne-Edwards.

We shall divide the evidences on either side under two heads; the first, that which is derived from an external observation; and the second, that which is derived from its internal organization.

First then from external circumstances: An auditory apparatus is an organ furnished to an animal for one or both of two objects; first, for protection from danger; secondly, for the plea-

* This will be more enlarged upon in the forthcoming Report at the next Meeting of the British Association.